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Communicated January 18th 1965 by SVEN SEGERSTRÅLE

HELSINKI – HELSINGFORS 1965

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Introduction

In the northern Baltic area there are three species of marine bivalves, *Mytilus edulis* L., *Macoma baltica* (L.) and *Mya arenaria* L., and one brackishwater species, *Cardium lamarcki* Reeve. Some years ago the opinion still prevailed that *Cardium edule* L. was the fourth bivalve species occurring in our waters. However, this opinion changed after the publication of Høpner Petersen's (1958) paper on the biology and distribution of the species of *Cardium* living in Danish brackish waters. According to this paper *Cardium edule* is a marine species which does not occur in waters with a salinity below 20—25‰, while *Cardium lamarcki* is a brackishwater species whose salinity amplitude extends from c. 25‰ to c. 5‰. Accordingly, *C. edule* cannot exist in the Baltic proper. That the species living in Finnish waters is *C. lamarcki* was confirmed by Koli (1959). Older notes on *C. edule* in the Baltic proper consequently refer to *C. lamarcki*.

In his investigations on *Macoma baltica* Segerstråle (1927, 1933 *b*, 1960 *b*, 1960 *c*, 1962) has studied problems connected with the recruitment and population dynamics of this species. The same author (1933 *b*) also provided some information about our other bivalve species. Further notes on our marine bivalves have been published mainly by Tulkki (1960, 1964) and Koli (1961).

»Plankton-tables for Finland» (Levander 1903—1911) is an important source of information concerning the distribution of bivalve larvae in the inner Baltic. These tables are a primary source of material hitherto seldom used (but cf. PURASJOKI 1945, 1958, LINDQVIST 1958 *a*, 1959, 1961). The records of bivalve larvae in these tables have not been analysed before. Valuable information is also provided by an extensive table of data for a still unpublished paper on the Baltic plankton. These tables were kindly placed at my disposal by K. J. PURASJOKI, Ph.D., (Tvärminne Zoological Station, University of Helsinki). The occurrence of bivalve larvae in the area in question has further been discussed by a number of authors, particularly VÄLIKANGAS (1926), HESSLE & VALLIN (1934), LEVANDER & PURASJOKI (1947), HALME (1958, 1960) and LINDQVIST (1959). In all the papers hitherto published the larvae have been treated collectively, without separation of the species.

In order to increase our knowledge concerning the early developmental stages of our bivalves, I started an investigation in 1958 at Tvärminne Zoological Station (S. W. Finland), intending to study the settling of the different species in temporal and quantitative respects. In connexion with this work I had to consider a number of questions associated with the distribution of the bivalves in the whole northern Baltic area, as well as the occurrence of their larvae in this area. The present paper is based upon these latter studies.

The northern Baltic area

The Baltic is divided into a number of subareas. Some of these are basins, clearly separated by sills, while the natural limits of others are more diffuse. While the German nomenclature on the Baltic subareas has reached some stability (see EKMAN 1931, WATTENBERG 1949) the English terminology is still rather fluid. According to EKMAN (1931, p. 171), the Baltic proper (»die eigentliche Ostsee») comprises the part of the Baltic inside the Belt Sea excluding the Gulf of Bothnia, the Åland Sea, the Archipelago Sea, the Gulf of Finland and the Gulf of Riga (Fig. 1).

The Gulf of Bothnia is divided into two basins by the shallow Quark: the (northern) Bothnian Bay and the (southern) Bothnian Sea. The Åland Sea, between the Bothnian Sea and the Baltic proper, is deep, while the Archipelago Sea, between Åland and the Finnish mainland, is mostly shallow. In the northeast the basin of the Central Baltic continues into the Gulf of Finland. The Gulf of Riga is joined to the northern Baltic proper. In the present paper the »northern Baltic area» comprises the Gulf of Bothnia, the Åland Sea, the Archipelago Sea, the northern part of the Baltic proper and the Gulf of Finland.

The salinity of the Baltic is relatively stable in each region. In coastal waters conditions are subject to greater fluctuations than in the open sea,

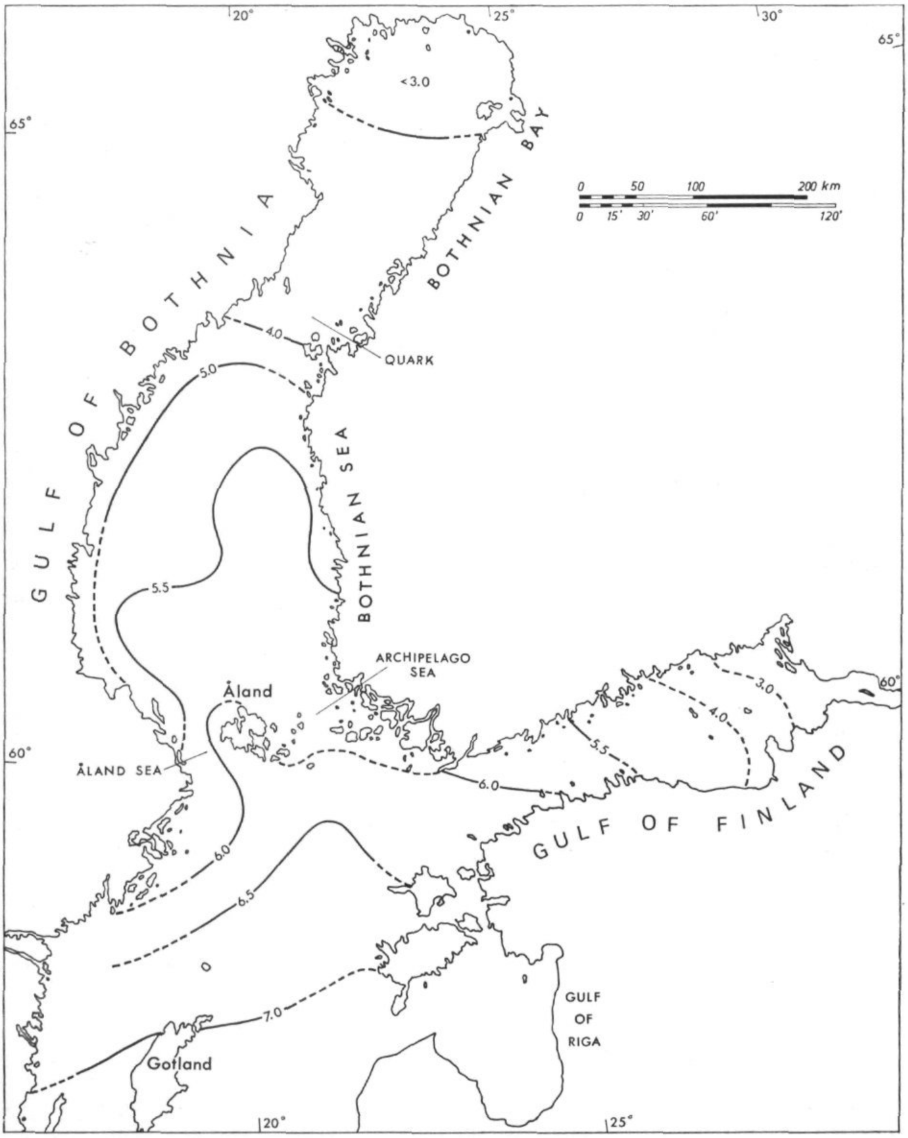

Fig. 1 Chart of the northern Baltic area. The surface isohalines ($^0/_{00}$) mainly follow the July isohaline for 1954–1956, as shown in the Atlas of Finland 1960. Those for the easternmost part of the Gulf of Finland were taken from the 1925 edition. The $7^0/_{00}$ isohaline is based on unpublished data of the Institute of Marine Research, Helsinki/Helsingfors.

especially in the vicinity of rivers, where the surface layer may be highly diluted beneath the ice during the winter (see e.g. SEGERSTRÅLE 1951 *b*). The greatest fluctuations occur in the innermost parts of the Gulfs of Finland and Bothnia. The mean surface isohalines ($^0/_{00}$) of the northern Baltic area are shown in Fig. 1.

In the Baltic proper and in the Gulf of Finland the water mass is constantly stratified. At a depth of 60–80 m there is a permanent halocline below which the water is more or less stagnant and often poor in oxygen. Above this, the circulation is more intense and the oxygen conditions satisfactory. The heavier bottom water of the Baltic proper does not as such flow into the Åland Sea and the Gulf of Bothnia. In the latter areas the vertical exchange of water is great, and the bottom water is often renewed, so that the oxygen conditions are generally good from surface to bottom.

The seasonal temperature fluctuations are great in the Baltic. Ordinarily the water is warmest in August. There are often considerable temperature changes in the summer, owing to changing wind conditions. In the whole northern Baltic area at least the coastal zone is ice-covered in the winter, while the Central Baltic is ice-covered only at the height of extremely cold winters.

According to BUCH (1945), the pH of the surface layer decreases northwards in the area. Below the halocline in the Central Baltic and the Gulf of Finland the pH is low (Table I).

Table I. pH values for the northern Baltic (mean values for 9 years). (Buch 1945.)

	surface	bottom
Northern part of the Central Baltic	8.26	7.08
Gulf of Finland	8.39	7.09
Bothnian Sea	8.20	7.54
Bothnian Bay	8.06	7.57

The horizontal surface currents in the area mostly form systems of counterclockwise gyres (Fig. 2), although there may be considerable deviations from this pattern.

For further information on the hydrography of the northern Baltic area, see the »Atlas of Finland» (1910, 1925, 1960), Merentutkimuslaitoksen julkaisu / Havsforskningsinstitutets skrift (1920–), VÄLIKANGAS (1933), GRANQUIST (1938), BUCH (1945), JURVA (1952), SEGERSTRÅLE (1957) and PURASJOKI (1958).

For general information on the flora and fauna of the Baltic, see VÄLIKANGAS (1933), SEGERSTRÅLE (1957) and ZENKEVITCH (1963).

Fig. 2 Chart of the average horizontal surface currents in the northern Baltic area. 1 mm vector length corresponds to a current velocity of 0.5 cm/sec. The stability of the currents is indicated by the numbers 0–100. 100 stands for current with unchanging direction of flow, 0 for current returning the water particle to its original point of departure. (Palmén 1930.)

The horizontal distribution of postlarval lamellibranchs

Our knowledge of the distribution of bivalves in the Gulfs of Finland and Bothnia is in many respects based upon records and investigations made during the 19th or early 20th century. This statement applies especially to the south coast of the Gulf of Finland. The records on the innermost finds of the bivalves of the northern Baltic area are listed below (cf. Fig. 3).

Mytilus edulis

Gulf of Bothnia, W. coast: From the summer of 1963 there is a record of small (c. 5 mm) *Mytilus* occurring at Gerdasgrund, south of Holmögadd, at 7–11 m depth in the Quark (BERGH 1964). The northernmost locality from which the species was known previously was off the island of Ulvö

(MUNTHE 1895, p. 8) about 65 nautical miles to the southwest of the new locality.

Gulf of Bothnia, E. coast: According to NORDENSKIÖLD & NYLANDER (1856, p. 99), *Mytilus* is distributed as far as Vaasa/Vasa. There is no detailed information about the locality. VALOVIRTA (1935) found the species off the island of Rönnskär, west of Vaasa. In the summer of 1963 it was found at Storgrund (63°09′30″N, 21°25′45″E) in the archipelago of Vaasa (Mr. S. PEKKARI, Lic. phil., Uppsala, Sweden, personal comm.)

Gulf of Finland: The island of Suursaari (Hogland) (VÄLIKANGAS 1933, p. 8).

Gulf of Finland, N. coast: Pellinge/Pellinki (SEGERSTRÅLE 1944).

Gulf of Finland, S. coast: Monk-Wiek (Eru laht) (Книповичъ 1909, p. 0222). KOJEVNIKOV (1892, p. 20), giving SCHRENK (1848) as his source, reports Narva as the easternmost locality. However, the latter author does not mention anything about *Mytilus edulis*, for which reason KOJEVNIKOV's report seems dubious.

Cardium lamarcki

Gulf of Bothnia, W. coast: The island of Brämö (ELOFSON 1952).

Gulf of Bothnia, E. coast: The archipelago of Valsörarna (Valassaaret) and the island of Rönnskär (finds of empty shells in 1953, O. HILDÉN and E. HÄYRÉN respectively, cf. SEGERSTRÅLE 1955). In the summer of 1963 the species was found living amongst red algae at Nygrund (63°07′45″N, 21°20′E) in the archipelago of Vaasa (PEKKARI, cf. BERGH 1964).

Gulf of Finland, N. coast: In June 1964 empty shells were found off the island of Kuutsalo (60°28′N, 27°05′E), southwest of Kotka (2 m depth, sandy bottom), according to information kindly given by the Fisheries Foundation (Kalataloussäätiö-Fiskeristiftelsen). The easternmost find of living specimens is from the archipelago of Aspskär, commune of Pernå/Pernaja (KOSKIMIES 1957, p. 53).

Gulf of Finland, S. coast: Narva (KOJEVNIKOV 1892, p. 20). The same comment as for *Mytilus* (cf. above) pertains to this report also. Because of this, SEGERSTRÅLE (1933 *b*, p. 13) has thrown doubt upon the report. If KOJEVNIKOV's report is incorrect, Tallinn (Reval) (SIEMASCHKO 1847, p. 126, KOJEVNIKOV 1892, p. 20) would be the easternmost locality from which records of *Cardium* have been published. In view of the salinity conditions, however, it is probable that the species is distributed farther eastward than this.

Macoma baltica

Gulf of Bothnia, W. coast: Ratan (HESSLE 1924, p. 13, BERGH 1964)

Gulf of Bothnia, E. coast: Hailuoto (Karlö) (empty shells on the shore)

(SEGERSTRÅLE 1960 *a*). The northernmost find of living specimens is from off Kokkola/Gamla Karleby (NORDQVIST 1890, p. 89).

Gulf of Finland, N. coast: Commune of Koivisto (Björkö) at the entrance of Vyborg Bay (shells on the shore, E. QUARNSTRÖM 1896, cf. LUTHER 1909, p. 9). SUOMALAINEN (1939) found the species living in the same area.

Gulf of Finland, S. coast: Peterhof (SIEMASCHKO 1847, p. 127). The record seems not to have been noticed before by Finnish scientists. If it is correct, *Macoma* occurs (or has periodically occurred) much farther east in the Gulf of Finland than is generally supposed. Книповичъ (1909, p. 0227) found the species somewhat north (60°05'N, 21°21'E) of Seiskari (Seitskär).

Mya arenaria

Gulf of Bothnia, W. coast: There are no published records; the northernmost find on the Swedish coast is from the archipelago of Stockholm (HÄGG 1953).

Gulf of Bothnia, E. coast: The bay of Töjbyviken (62°36'N) (NORDQVIST 1890, p. 101).

Gulf of Finland, N. coast: Commune of Sibbo/Sipoo (NORDENSKIÖLD & NYLANDER 1856).

Gulf of Finland, S. coast: Narva (KOJEVNIKOV 1892, p. 21). SEGERSTRÅLE (1933 *b*, p. 20) has thrown doubt upon the report (cf. notes above for *Mytilus* and *Cardium*). If KOJEVNIKOV's report is incorrect, Tallinn (Reval) (SIEMASCHKO 1847, p. 130, KOJEVNIKOV 1892, p. 21) would be the easternmost locality from which records of *Mya* have been published. Judging by the salinity conditions and the distribution of the species off the coasts of Finland, however, it is probable that *Mya* occurs farther eastward than this.

DISCUSSION

The innermost localities where the species are found must naturally not be considered categorical limits. The limits of distribution are, of course, never entirely sharp, but the populations diminish and finally cease. This more or less distinct border zone may be displaced in one direction or the other, depending on changes in the ecological conditions (it is probably a case of the interaction of many factors, of which salinity plays the major part). In favourable years the bivalve populations may thus extend further up the Gulfs of Finland and Bothnia, retreating again during less favourable periods.

Taking into consideration the relation between salinity and the dis-

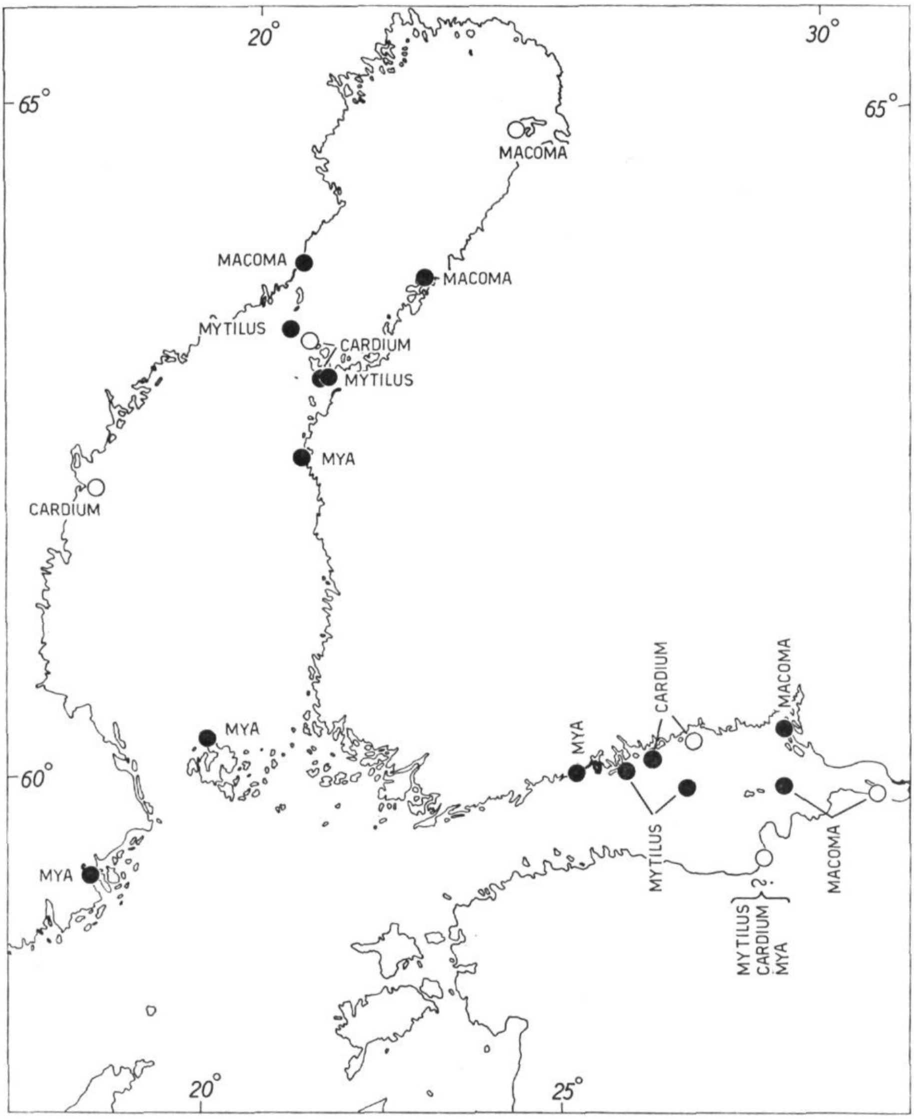

Fig. 3 The innermost finds of the lamellibranchs *Mytilus edulis*, *Macoma baltica*, *Cardium lamarcki* and *Mya arenaria* in the northern Baltic area. Empty circles refer to finds comprising, or presumed to comprise, shells only. Compiled from various sources, cf. text.

tribution of *Macoma* in the Gulf of Finland, one might have expected this species to be common in those parts of the Bothnian Bay with similar salinity conditions. However, there is a discrepancy between the two areas, the species occurring regularly only in the south parts of the Bothnian Bay. SEGERSTRÅLE (1962, p. 18) has suggested the reason for the absence of

Macoma in the deep parts of the Bothnian Bay to be the low temperature, which is presumed to be lethal to settling larvae. Further he suggests a negative effect of the humic substances carried into this area by rivers.

Amongst our bivalves *Macoma* is the most tolerant of low salinity and *Mya* the least tolerant. It is considerably more difficult to compare the salinity tolerance of *Mytilus* and *Cardium*. *Mytilus* is found somewhat further up the Gulf of Bothnia than *Cardium* (the fact that on the Swedish side *Cardium* is not recorded from farther north than the island of Brämö is possibly due to lack of knowledge of the true situation). On the contrary, off the north coast of the Gulf of Finland, *Cardium* is found somewhat higher up than *Mytilus*. The find of *Mytilus* at the island of Suursaari is difficult to compare directly with the find of *Cardium* off Kotka and near the Aspskär Islands because the isohalines run obliquely (cf. Fig. 1)*) and because of the difference in time between the records. It is open to doubt whether one could attach great significance to records from different times and use them for comparative purposes, as a means of ascertaining to what degree the tolerances of the species differ from each other. A suggestion of the real relationships is perhaps given by investigations performed during a restricted period, and within limited areas in which the salinity conditions, generally speaking, are reflections of the conditions in the Gulfs of the Baltic. An area of that kind is Pojoviken in S. W. Finland, near the entrance of the Gulf of Finland. There *Mytilus* is found farther up (as far as Ekenäs) than *Cardium* (Källviken area) (Koli 1961). However, on the basis of our present knowledge it seems impossible to establish any real difference between *Mytilus* and *Cardium* in regard to their tolerance of dilution.

Thus it could be concluded, as regards the distribution of the species, that the lowest mean salinities at which they exist in the inner Baltic are as follows (corresponding values given in the recent literature are cited in parentheses):

Macoma baltica, 2—3‰, regular occurrence at c. 3.5‰ in the Gulf of Bothnia (3.5‰, Gulf of Bothnia, Hessle 1924, p. 30; 2.5—3‰, c. 3‰, Pojoviken, Koli 1961, pp. 12, 15; 2—3‰, Gulf of Finland, 3—4‰, Gulf of Bothnia, Segerstråle 1962, p. 18).

Mytilus edulis, 4.0—4.5‰, (4.0‰, Gulf of Bothnia, Hessle 1924, p. 30; 4.5—5.0‰, Gulf of Finland, Välikangas 1933, p. 81, Gulf of Finland and Bothnia, Segerstråle 1944, Pojoviken, Koli 1961, p. 15).

* For the same reason the uncertain records of *Mytilus* and *Cardium* off Narva (cf. pp. 8) cannot be dismissed as completely impossible, though the source reported by Kojevnikov is wrong. The corresponding record of *Mya* seems more unlikely, in the light of what is hitherto known of the distribution of this species along the coasts of Finland and Sweden.

Cardium lamarcki, 4.0—4.5‰, (4.5—5.0‰, Pojoviken, KOLI 1961, p. 18).

Mya arenaria, 4.5—5.0‰, (5,0‰, Gulf of Bothnia, VÄLIKANGAS 1933, p. 79; 4.5—5.0‰, Pojoviken, KOLI 1961, p. 15).

Since the time of the Littorina Sea the salinity of the Baltic has decreased considerably. The salinity reduction has led to great changes in the flora and fauna. As regards the marine molluscs, they have all been forced back. *Littorina littorea*, for example, which now occurs only south of Bornholm, was once distributed half way up the Gulfs of Finland and Bothnia (see e.g. MUNTHE 1895, SEGERSTRÅLE 1957). Of lesser amplitude, but biologically important are those salinity fluctuations (see e.g. GRANQVIST 1938, 1949, 1952, LISITZIN 1948, SEGERSTRÅLE 1951 *a*, 1953, AHLNÄS 1962) which have been observed since the hydrographical study of the Baltic was started. The period of increased salinity, which began in the late 30's, has especially attracted notice. The salinity increased on an average by 0.5 ‰ in the surface layer off the south coast of Finland. It has been stated that during this period the distribution areas of a number of species have widened. The most cited example is *Aurelia aurita* (ERKAMO 1942 *a*, *b*, VÄLIKANGAS 1942, PURASJOKI 1949, HÄGG 1950, HELA 1951, SEGERSTRÅLE 1951 *a*, *b*, 1953, 1957). PURASJOKI (1953) mentions a number of planktonic species: *Fritillaria borealis* (Appendicularia), *Temora longicornis*, *Pseudocalanus elongatus*, *Centropages hamatus* (Copepoda). For the same reason *Calliopius laeviusculus* (Amphipoda) extended its distribution inwards towards the coast in the Tvärminne area (SEGERSTRÅLE 1953). According to ELOFSON (1952), *Balanus improvisus* (Cirripedia) penetrated northward along the west coast of the Gulf of Bothnia, and the same was the case with the cod (*Gadus callarias*) and the sprat (*Clupea sprattus*) (ALANDER 1952). LINDQUIST (1958 *b*, 1959) found that the composition of the zooplankton in the Bothnian Sea had changed. In regard to the lamellibranchs, however, there are very few notes on expansion due to the increased salinity. ELOFSON (op. cit.) connects the record on *Cardium* off Brämö (cf. p. 8) with the salinity increase. An eastward extension of the distribution of *Astarte borealis* and *Cyprina islandica* in the southern Baltic was, according to MAŃKOWSKI (1951, p. 116), due to the same phenomenon.

In the summer of 1958, once, when dredging algae in Tvärminne, the yield consisted almost exclusively of a mass of *Mytilus* on a bottom (west of the islet of Skarvkyrkan) which, according to Dr. K. J. PURASJOKI (personal comm.), was earlier known as a good bottom for algae without »disturbing» amounts of *Mytilus*. A plausible reason for the strong increase of *Mytilus* would be the increased salinity, although other circumstance may have been conducive to a particularly successful recruitment during some years.

It may be further mentioned that, according to SEGERSTRÅLE (1951 *b*,

p. 7) in the archipelago of Pellinge/Pellinki (c. 26°E) *Mytilus* lives so near to its eastern limit in the Gulf of Finland that a slight decrease of the salinity would exclude the species from the inner waters of the area. The fact that *Macoma* can exist in the innermost parts of the Gulf of Finland, though during the spring the water is almost completely diluted, is, according to the same author, due to the fact that reproduction takes place mainly in the summer, when the salinity is higher (SEGERSTRÅLE 1951 *b*, p. 26). The report on the occurrence of *Macoma* off Peterhof (cf. p. 9) may possibly be considered reliable for the same reason, in spite of the great outflow of fresh water from the river Neva. Of course, we know nothing about the hydrographical conditions in the middle of the last century. But it seems unlikely that conditions at that time differed essentially from those prevailing at present.

There is little written about the salinity conditions during the last decade. SEGERSTRÅLE (unpubl.) has studied the salinity records (at 5 m depth) for Russarö and Tvärminne at the entrance of the Gulf of Finland, and for Harmaja/Gråhara off Helsinki. Prof. SEGERSTRÅLE has kindly shown me his salinity diagrams, from which the following facts may be seen. The salinity was fairly low in 1954—1960, although still higher than before the increase began in the 30's. The average salinity for 1961 was again high but it decreased during 1962. As regards the biological consequences of these phenomena there are still no comments.

Temperature is one of the cardinal factors in ecology, and often of decisive significance. In the shallow waters of the northern Baltic area, down to moderate depths (15—20 m), the temperature will probably not be a minimum factor for adult bivalves, except during the winter in the freezing zone, where to a great extent the temperature acts indirectly through the mechanical effect of the ice. Another indirect effect of temperature can be seen in very shallow waters, where the ice lies close to the bottom. In such places lack of oxygen tends to set in. At greater depths the situation is altogether different, and will be discussed below.

The vertical range of the lamellibranchs in the northern Baltic area

As is known, many marine species widen their vertical range in the Baltic proper. Amongst our bivalves this applies primarily to *Macoma* and *Mytilus*, and to some extent *Mya* and the brackishwater species *Cardium*. At the present stage of our knowledge it is not possible to be precise as to how far the vertical distribution of these species is due to physiological and ecological requirements and how far to the behaviour of the larvae. In most cases we are only able to establish some contributory causes.

Below the halocline (cf. p. 6) in the Central Baltic and western Gulf of Finland, wide areas are at present almost without life owing primarily to hydrographical conditions. SHURIN (1964) has found that in the east and north parts of the Central Baltic the quantity of benthos is steadily declining, in spite of a somewhat improved ozygen régime during recent years. But also above the halocline in these areas and in the Gulf of Bothnia, where the oxygen conditions are satisfactory, the bivalves in question mainly live in shallow water.

In regard to *Mytilus* and *Macoma* in the Baltic the temperature will probably not, in any case not directly, be a limiting factor for adults. On the other hand, it may be assumed (SEGERSTRÅLE 1962, p. 18) that the low temperature which characterizes the deeper parts of the Bothnian Bay would have a lethal effect on settling larvae of *Macoma* (cf. p. 11). According to JOHANSEN (1918, p. 653), in the Deeps of Bornholm and Gdansk the oxygen supply and other physical and chemical factors regulate the vertical distribution of *Mytilus* and *Macoma*. According to the same source, both penetrate deeper into the better ventilated Deep of Gdansk than into the Deep of Bornholm. At present we can ultimately ascribe the total lack of these species in the deeper parts of the Baltic proper and the Gulf of Finland to unfavourable hydrographic conditions, mainly insufficiency of oxygen (cf. above).

As far as *Macoma* is concerned, the cause, according to SEGERSTRÅLE (1960 *c*, 1962), is different in the inner Baltic. SEGERSTRÅLE has developed an idea suggested by HESSLE (1924). The active factor is not hydrographic but biotic in nature. Dense populations of *Pontoporeia affinis* and *P. femorata* (Amphipoda) seem to kill off young postlarval *Macoma*. Where *Pontoporeia* is very abundant, i.e. in deeper water, *Macoma* is lacking or sparse. However, in the relationship between *Macoma* and *Pontoporeia* temperature indirectly plays a rôle. In deep water *Macoma*, partly owing to the low temperature, grows so slowly that the stage susceptible to *Pontoporeia* lasts longer than in shallow water (SEGERSTRÅLE 1960 *b*, 1962). Thus, although *Macoma* has the widest vertical amplitude of the bivalves occurring in the northern Baltic area, this species, too, occurs mainly in shallow water. In the Tvärminne area the number of individuals per unit area is generally greatest above the 10 m line (see SEGERSTRÅLE 1933 *b*, 1960 *b*). In the Airisto Sound the maximum abundance is said to be between 5 and 10 m (TULKKI 1960, p. 13). In Swedish waters HESSLE (1924, p. 13) found a greater abundance at 0—10 m than at a depth of 11—50 m. The greatest depth from which *Macoma* has been taken in the northern Baltic is 200 m (TULKKI 1960, p. 13).

A reason limiting, though not wholly preventing, the occurrence of *Mytilus* in deep water is the lack of a firm substrate. When the abundance of the mussel is to be estimated at different depths, one difficulty is that conventional quantitative gear does not function satisfactorily on hard bottoms. Probably the species is more abundant in rather deep water than indicated by the numbers obtained by sampling with bottom grabs. However, there is no doubt that the main distribution of *Mytilus* is in shallow water. In the Tvärminne area *Mytilus* occurs chiefly at depths of 1—15 m (KOLI 1961, p. 11). In the Airisto Sound (S.W. Finland, the archipelago of Turku/Åbo) TULKKI (1960, p. 14) found the highest density between 5 and 10 m. In the Tvärminne area the species was taken at a maximum depth of 35—36 m by SEGERSTRÅLE (1933 *b*, Table I), and at 18 m by KOLI (1961, p. 11). In the Lohm area (S.W. Finland), BAGGE, JUMPPANEN, LEPPÄKOSKI & TULKKI (1965), have recorded *Mytilus* from a depth of 53 m. HESSLE (1924) found it in the archipelago of Stockholm at 40 m (op. cit., Plate V D) and off the island of Gotland (N.W. coast) at 70 m (op. cit., p. 20). It must be noted that many of the finds of *Mytilus* in deep water consist of individuals that have drifted down from higher levels. BRAUN (1884, p. 118) gives c. 40 m (22 fathoms) as the maximum depth for *Mytilus* in the Gulf of Finland.

The main distribution of *Cardium* is above 10 m depth (cf. HESSLE 1924, p. 19, SEGERSTRÅLE 1933 *b*, p. 12, TULKKI 1960, p. 20, KOLI 1961, p. 12). In the Tvärminne area SEGERSTRÅLE (1933 *b*, p. 12) has taken the species at a maximum of 18—21 m, and KOLI (1961, p. 12) at 11 m. In the Lohm area it occurs at a maximum of 15 m (BAGGE et al. 1965). HESSLE did not find it at all below the 10 m line. BRAUN (1884, p. 118) gives c. 36 m (20 fathoms) as the maximum depth for *Cardium* in the Gulf of Finland.

For the vertical distribution of *Mya* the temperature may be a factor to consider. According to BELDING (1916, as cited by NEWCOMBE 1935, p. 128), the growth of *Mya* continues down to a temperature of about 5°. It has been experimentally established (LOOSANOFF & DAVIS 1963, p. 125) that the species also needs a relatively high temperature during its larval stage. In a temperature as high as c. 14° the larvae grew slowly. Though LOOSANOFF & DAVIS worked in another area, I think we can assume that cold water is unfavourable for *Mya* in the Baltic too. Thus the conditions in the deeper layers would be adverse to the species, principally to the metamorphosing larvae and to the spat. For it is known that in many marine invertebrates the early bottom stages are more sensitive to extreme temperatures than the later larval stage, and that the latter is more sensitive than the adult stage (for references, see THORSON 1946, p. 423; cf. p. 11, *Macoma*). The sparse occurrence of sandy bottoms in deeper waters will probably not radically limit the vertical distribution, as *Mya* lives on mud bottoms too. The main distribution in the Tvärminne region is above the 10 m line. In the same area KOLI (1961, p. 12) has found the species down to 15 m depth, the same depth at which it is taken in the

Aiiisto Sound (TULKKI 1960, p. 13). According to BRAUN (1884, p. 118) the maximal depth for *Mya* in the Gulf of Finland is c. 18 m (10 fathoms). In Swedish waters HESSLE (1924, p. 20) has found it at a maximum of 13 m.

Another fact to be mentioned in this connexion is the amount of food in the water. One might expect that the suspension feeders *Mytilus*, *Cardium* and *Mya* would find the most favourable conditions in shallow water, where the density of phytoplankton should be the highest. Of these species *Mytilus* is the only one which occurs at greater depths (cf. pp. 14—15). There are very few quantitative investigations on the phytoplankton of the northern Baltic area. According to HALME & MÖLDER (1958), who have studied the area from Pojoviken to Tvärminne in this respect, the difference in the amount of phytoplankton in the epilimnion and the hypolimnion is rather slight during the greater part of the year (deepest station: c. 35 m). However, the greatest density differences occur in the summer, which is the main period of growth for the bivalves. Accordingly, the nutrition factor may be a contributory limiting factor in deeper waters, but there is still very little known about this in our waters.

As regards the deposit-feeding *Macoma*, SEGERSTRÅLE (1962, pp. 61—62, cf. also 1933 *a*, p. 30) suggests that the mud in deeper water has a low nutritive value, and that such localities are thus less favourable than shallow and sheltered localities.

It is well known that many lamellibranchs react in some way to light; however, little is known about the ecological consequenses of the reactions as regards the vertical range of these animals. The light conditions seem in general to be treated as unimportant in this respect. According to DOGSON (1928, p. 193) pumping is disturbed in *Mytilus* by rapid changes of light. The mussel opens and functions best in the dark, or in very subdued daylight, especially if the temperature is low. COULTHARD (1929) showed that the growth rate of *Mytilus* is greater in shade and darkness than in full sunlight. Accordingly, lack of light will not impede this species in deep water. The siphons of *Cardium edule*, a species nearly related to *C. lamarcki*, retract if a shadow is rapidly thrown on the animal (JOHNSTONE 1899, p. 60). Intensity and wave-length of light have effect upon the reactions of the siphons also in *Mya arenaria* (see e.g. HECHT 1921, 1924, 1927, HECHT & WOLF 1932). See also NAGEL 1894, WENRICH 1916, HUNTSMAN 1921, PIERON 1926.

Neither is much known about the influence of pressure in comparatively shallow waters such as the Baltic.

For the vertical distribution of the bivalve larvae, see p. 31.

The distribution of lamellibranch larvae

The investigations performed by AURIVILLIUS (1896) on the temporal occurrence of the most important zooplankton species form an important contribution to our knowledge of the Baltic plankton. His material was collected in 1894 (three times each month) at four Swedish lightships. Three of these stations fall within the area with which this paper is concerned. These were Sydostbrotten (63°21'N) in the Quark, Grundkallen (60°30'N) in the southernmost part of the Bothnian Sea and Kopparstenarne (58°35'N) north of the island of Gotska Sandön.

»Plankton-tables for Finland» (Levander 1903—1911) are my most important source of data. Some explanatory words about this material are necessary before an account is given of the occurrence of lamellibranch larvae in the subareas of the inner Baltic. Levander's tables are based on a long series of plankton samples taken at the permanent F stations in the area during the years 1903—1911. The tables have been published as primary material without comments. The abundance was estimated. The lamellibranch larvae were treated collectively, as in all hitherto published papers on the plankton of the northern Baltic area. The samples were taken mainly in February, May, August and November, though partly also in January, March, June and October. Because of this I have divided the material in the tables into four groups: »Winter» (Jan., Febr., March), »Spring» (May, June), »Summer» (July, August) and »Autumn» (Oct., Nov.). A map is given for each season (Figs. 5—7). The maps are plotted according to a system similar to that used by Purasjoki (1945) in regard to *Fritillaria borealis* and Lindquist (1958 *a*) in regard to *Pleurobrachia pileus*. The positions of the stations appear in Fig. 4.

As regards the primary tables which Dr. Purasjoki has placed at my disposal, they refer to material collected partly during a cruise in the northern Baltic area (F stations) in July 1964 (unpubl. tables, *a*), partly during the years 1950—1953 at the lightships Norströmsgrund, Finngrundet, Hävringe and Helsinki, and off the island of Jungfruskär (unpubl. tables, *b*). For the location of the stations, see Fig. 4. The net used in 1934 was of the Apstein type. The water mass from 20 m depth to the surface was sampled in 4 vertical hauls (20—15, 15—10, 10—5, 5—0 m), while the samples from below 20 m were taken with rather varying depth limits. Each vertical metre of haul should correspond to 5 litres of water sieved. Fig. 8 shows the occurrence of lamellibranch larvae in the layer above 20 m in July 1934, while the vertical distribution is shown in Fig. 10. In 1950—1953 the nets used were of the Hensen type, but finer. These samples were taken vertically from 25 m to the surface. The occurrence of lamellibranch larvae according to this material is shown in Fig. 9. For further details on methods, see Purasjoki (1958).

Below is an account, subarea by subarea, of the occurrence of bivalve larvae in the northern Baltic area. The subareas will be treated in the following order: Bothnian Bay; Bothnian Sea; Åland Sea, Archipelago Sea and the northern part of the Baltic proper; Gulf of Finland.

BOTHNIAN BAY

The Bothnian Bay is rather incompletely investigated. During his investigations in July and August 1887 NORDQVIST (1890) did not find any bivalve larvae. It is true that the area investigated extended from the Quark to the innermost end of the Bay, but the samples were few and the work almost had the character of a superficial inventory. However, neither did LEVANDER find any larvae in the area during the long period 1903—1911. In samples from the islet of Ulkokalla (64°20′N, 23°27′E) taken from May to October 1910 they are likewise lacking (LEVANDER & PURASJOKI 1947). WUORENTAUS (1913) did not find any lamellibranch larvae off Siikajoki, Hailuoto (Karlö) or Raahe (Brahestad) (mid-June to mid-Sept., 1911). Plankton investigations performed by HESSLE & VALLIN (1934) in the western parts of the Bothnian Bay in 1926—1927 agreed with the earlier investigations. At the end of July 1934 there were no finds of lamellibranch larvae at about ten F stations (Fig. 8) which satisfactorily covered the Bothnian Bay (PURASJOKI unpubl. tables, *a*). Plankton samples from the lightship Norströmsgrund in the northwestern part of the Bothnian Bay (Fig. 4) were just as negative. They were taken in two periods, 1952 (end of Aug. to mid-Nov.) and 1953 (beginning of June to beginning of Dec.) (PURASJOKI unpubl. tables, *b*).

Consequently, in the Bothnian Bay lamellibranch larvae have not been found either before or during the period of increased salinity.

BOTHNIAN SEA

In the Bothnian Sea lamellibranch larvae may occur rather commonly. NORDQVIST (1890) reports that he found such larvae in the summer of 1887. AURIVILLIUS (1896) did not find any bivalve larvae in the summer of 1894 at Sydostbrotten (14.5.—12.11). At Grundkallen there were larvae at least on July 22, according to AURIVILLIUS — probably *Mytilus* larvae. According to LEVANDER's tables, lamellibranch larvae occur in the Bothnian Sea from spring to autumn, though not as regularly as in the Åland Sea, the Archipelago Sea, the northern part of the Baltic proper and the western Gulf of Finland. HESSLE & VALLIN (1934) found them (1926—1927) in the Bothnian Sea from the neighbourhood of the islands of Ulvöarna southwards. The finds were few and were made in July and October. In the middle of July 1934 there were, according to PURASJOKI's plankton records (unpubl. tables, *a*), lamellibranch larvae at least in the southern part of the Bothnian Sea (F 28—33) and in parts of the northern Bothnian Sea (F 21, 22, 24, and off Härnösand) (Fig. 8). In the Quark no larvae were found. The middle part of the area was not sampled. A series of samples from the lightship Finngrundet in the southern Bothnian Sea (Fig. 9), taken twice monthly from the end of August 1951 to the end of 1953 (with a short interruption in Feb. — March 1953) shows a sporadic occurrence of larvae in August 1951 and transiently at the end of June and beginning of July 1953. During the whole of the year 1952 there were no finds of lamellibranch larvae at all. PURASJOKI (in GRANQVIST 1955) found larvae of this kind sparsely off Mäntyluoto in mid-August 1954. LINDQUIST (1959) examined four cross sections of the Bothnian Sea between 61° and 63° N in 1956—1958. As a result of this he reported that lamellibranch larvae occurred in the area from the beginning of July to the middle of September with a maximum from the second half of July to the end of August (op. cit., p. 84).

The distribution of lamellibranch larvae in the Bothnian Sea is interesting. In a transect from Säppi (Säbbskär) to Agö (8.—9.6. 1927) HESSLE & VALLIN (1934, p. 70) noticed a marked difference in the composition of zooplankton as well as phytoplankton between the eastern and western parts of the transect. During recent investigations (LINDQUIST 1958 *b*, 1959) corresponding differences were found in the composition of zooplankton in the middle and southern parts of the Bothnian Sea. Sometimes the boundary was very sharp (LINDQUIST 1959, p. 128). Because HESSLE & VALLIN measured only small differences in salinity between the eastern and western parts of their transect, while the temperature was c. 2° higher in the eastern part, they supposed the differences in plankton composition to be due to the temperature difference. LINDQUIST (1959, p. 128) seems to be of the same opinion as regards the differences found by him.

As regards the bivalves, one finds from LEVANDER's tables that the larvae occurred more regularly along the east coast of the Bothnian Sea in the summer. The same seems to be the case in the autumn (Figs. 6—7). In the Quark this tendency cannot be seen. Also the abundance was higher in the eastern part of the Bothnian Sea than in the western part. HESSLE & VALLIN (op. cit.) do not give detailed data of their transect results, so it is not possible to know whether there were differences in the numbers of bivalve larvae between the eastern and western parts of the area. In July 1934, according to PURASJOKI's records (unpubl. tables, *a*), the larvae were more abundant in the eastern than in the western part of the Bothnian Sea, at least in the south (Fig. 8). During the investigations of LINDQUIST (1959, Fig. 17) bivalve larvae seemed to occur more densely in the eastern than in the western parts, except at the northern end of the Bothnian Sea, whereas generally (op. cit., p. 125) the amount of zooplankton was almost the same throughout the area.

Thus in the summer and autumn there is a tendency to a more regular occurrence and a greater abundance of lamellibranch larvae in the eastern part of the Bothnian Sea than in the western part. The explanation for these differences is probably to be found in a combination of causes, which will be discussed below.

The west coast of the Bothnian Sea has a different character from the east coast. On the Swedish side the coast falls steeply, especially in the northwest, to a relatively great depth. Shallow water areas (above 25 m) are very sparse along the west coast (cf. e.g. »Atlas of Finland» 1960), the zone well suited to bivalve colonization thus being much smaller along the Swedish than along the Finnish coast. Another fact to be noted might be the diversity in the distribution of postlarval bivalves (Fig. 3), which depends on the hydrographical differences between the east and west sides of the Bothnian Sea. As far as we know at present, on the west coast of the Bothnian Sea *Cardium* reaches its northern limit about midway between the Åland Sea and the Quark, while on the east coast it reaches high up into the latter area. *Mya* is not found at all on the Swedish side of the Bothnian Sea, and *Macoma* is considerably nearer to its northern limit there than on the Finnish side. Also if the now applicable reports on the innermost finds later prove to be incorrect, the fact remains that the salinity conditions are less favourable in the western parts of the Bothnian Sea than in the eastern parts. Thus we can suppose, in the light of what has been stated above, that the production of larvae might be lower off the west coast than off the east coast of the Bothnian Sea.

A study of the currents offers a further explanation of the unequal distribution of lamellibranch larvae in the Bothnian Sea. Southeast of this area lies the Archipelago Sea, rich in shallow waters, where conditions are favourable for the growth of a rich stock of bivalves. With the northflowing current (Fig. 2) larvae are probably transported from here along the east coast of the Bothnian Sea.

We have to reckon with a normal length of 2—4 weeks for the larval stage of our lamellibranchs (see Thorson 1946, 1961). The maximum mean velocities of the northward currents in the southern part of the Bothnian Sea, as given by Witting (1912 *a*, p. 54) and Palmén (1930) in their current charts, reach about 2—3 cm/sec. This corresponds to 1.7—2.6 km per day, which in a period of 2 weeks would mean a distance of about 24—36 km, and in 4 weeks 48—72 km. This seems to be too small to explain the differences in the distribution of the larvae. However, velocities of about 10 cm/sec. must be frequent (cf. Palmén 1930, Tables 9—12) during shorter periods. According to Voipio (1964, p. 51) the rate of the water transport from Utö in the northern Baltic proper to Valsörarna (Valassaaret) in the Quark varies from 2.6 cm/sec. to 6.2 cm/sec. These values reflect the transport of the water masses, not the surface current as such. Values exceeding 5 cm/sec. are presumably enough to explain the difference in the distribution of lamellibranch larvae in the Bothnian Sea. A velocity of 5 cm/sec. would mean a distance of c. 60 km in two weeks and c. 120 km in four weeks. Moreover, it is conceivable that the larvae may prolong their larval life if they do not find a suitable substrate for settling and metamorphosis (THORSON 1946, p. 465, MOORE 1958).

We should not accept the published mean velocities of the currents as proof of the absence of quicker modes of transportation. The fact that lamellibranch larvae are found in the open, deep parts of the Baltic, far from stocks of bottom-living mussels, shows that transport must have occurred, and the only reasonable explanation is transport by currents.

Hence, the unequal distribution of lamellibranch larvae in the Bothnian Sea would be due to:

a) A northward transport of larvae from the rich stocks in the Archipelago Sea, and from the coastal waters north of it.
b) A difference in production of larvae between the eastern and the western parts of the area.

In the northernmost part of the area the differences tend to even out. The reasons for this may be as follows:

a) Because of the slow speed of the current and the normally relatively short larval life of the lamellibranchs, larvae from the Archipelago Sea will not reach the northern parts of the Bothnian Sea. Moreover, the current in the northern part of the Bothnian Sea generally runs northwards with decreased stability (PALMÉN 1930, Fig. 2, or »Atlas of Finland» 1960).
b) The northward current turns westward, thus distributing larvae in this direction.
c) Because of the westward turn of the current the hydrographical conditions are equalized in the Quark.
d) The production of larvae in the shallow Quark. These larvae are suggested to be transported mainly in a southern direction along the Swedish coast.

In the open sea there has been very little regular plankton sampling in the spring and early summer. However, according to LEVANDER's tables, in the spring (Fig. 5) another type of distribution difference prevails than that described above. During this season there was a sharp distribution boundary between the Bothnian Sea and the areas south of it, bivalve larvae occurring only rarely in the Bothnian Sea (cf. p. 23).

ÅLAND SEA, ARCHIPELAGO SEA AND NORTHERN PART OF THEBALTIC PROPER

During the first half of July 1887 NORDQVIST (1890) found bivalve larvae in the Archipelago Sea, in Lumparen bight and in the Åland Sea. By the lightship Kopparstenarne, north of the island of Gotska Sandön, AURIVILLIUS (1896) in 1894 (12.5.—10.10.) found lamellibranch larvae on July 29 and on August 17. According to the plankton tables of LEVANDER (1903—1911) larvae occurred from spring to autumn (Figs. 5—7) and very regularly during the summer. There seems to be a certain tendency to sparser occurrence at the southernmost stations. In the Åland Sea HESSLE & VALLIN (1934) observed them from June till August (sampling: June—August 1926; February, June—October 1927). LEVANDER & PURASJOKI (1947) give records from off the island of Utö (1900, 1904—1906) and from the vicinity of the islet of Bogskär (1910). At Utö larvae were found from June till December, at Bogskär from May till December, with an interval from September to November (sampling: 20.5. — 19.12.). According to PURASJOKI (unpubl. tables, *a*) the occurrence of larvae was fairly rich both in the Åland Sea and in the northern part of the Baltic proper in the middle of July 1934 (Fig. 8). For the island group of Jungfruskär in the Archipelago Sea (Fig. 9) we have (PURASJOKI unpubl. tables, *b*) the records of a long series of plankton samples for the period October 1950 to December 1953. Most of the stations were sampled three times a month. In regard to Jungfruskär it can generally be said that bivalve larvae occurred from June to August. Occasional finds in October, November, December and January were noted. A similar series of samples (Dec. 1951 to Dec. 1953, twice a month) from the lightship Hävringe (Fig. 9) in the northern part of Baltic proper, off the east coast of Sweden, shows an occurrence of larvae more or less synchronous with that at Jungfruskär. However, there was a considerable quantitative difference, the larvae being more numerous at Jungfruskär.

Reports agreeing with those above are given by RIIKOJA (1925, 1928, 1929, 1931) for a number of stations in the northern part of the Baltic proper and the Gulf of Riga. RAPOPORT (1929), who studied surface plankton at 16 stations in the Gulf of Riga and neighbouring areas during the whole of 1925, did not, surprisingly, find any lamellibranch larvae. BĒRZIŅŠ (1932) did not find any larvae from May 8—25 in the year 1928 in the Gulf of Riga, which was probably due to the season.

GULF OF FINLAND

According to »Plankton-tables for Finland», lamellibranch larvae occurred in spring, summer and autumn, whereas in winter no larvae were found (Figs. 5—7). They were, as always, most regularly found in the summer. The larvae occurred most frequently in the western part of the Gulf of Finland, which is to be expected, in view of the salinity conditions and the distribution of the postlarval stages. There seems to be a certain difference between the seasons with regard to the distribution of the larvae. Especially in the spring there was sometimes, according to the tables, a remarkable difference between the eastern and western parts of the Gulf (cf. p. 21). In autumn the larvae seemed to reach farthest to the east.

Levander & Purasjoki (1947) give data from the following stations in the Gulf of Finland: Hangö/Hanko (1903—1910), Tvärminne (1904, 1907—1910), Porkala (1903—1906), Porkala area (irregular samples from different localities, 1901—1903, 1905), Långvik (1901), Gråhara (Harmaja) (1910). Generally lamellibranch larvae were observed from June to August, sometimes to September; in 1906, however, only till July at Porkala. In 1910 larvae appeared in the plankton at Gråhara between May 11 and 21. The spring of 1910 was the warmest recorded during the period 1900—1910 (Witting 1912 *b*). In some years larvae were found in small numbers later in the autumn, until December. Information in agreement with the above is given by Levander (1900, 1901, 1914, 1915, 1918) for different areas in the archipelago and near to the coast (the north coast of the Gulf of Finland, west of Helsinki/Helsingfors). In his investigations on the plankton of the harbour areas of Helsinki in 1919 Välikangas (1926) found lamellibranch larvae as early as May 7—8. During the summer they seemed to occur most abundantly in June, and then in decreasing numbers till the end of September or early October. There were no samples in the late autumn or winter. Riikoja (1925, 1928, 1929, 1931) studied the plankton of the Gulf of Finland as far as 27°47'E. The samples were taken in the summer (July—September) in the years 1925—1930. At times lamellibranch larvae occurred over the whole area. Between July 6 and 10, 1934, bivalve larvae were found (Fig. 8) from the entrance of the Gulf of Finland to somewhat beyond 27°E (Purasjoki unpubl. tables, *a*). Halme (1958, p. 59) found them in the area between Pojoviken and Tvärminne from May to December, with a maximum in June. The samples were taken from mid-June 1936 to the end of May 1937. The longest regularly taken series of plankton samples in the Gulf of Finland (Purasjoki unpubl. tables, *b*) completes earlier notes (the lightship Helsinki, Fig. 9; Nov. 1950 to Dec. 1953, twice a month). In 1950 bivalve larvae were found in November and December, in 1951 from mid-June to early October (maximum in June), in 1952 from mid-June to mid-September (maximum in June) and in 1953 in the beginning of February, during a relatively short period from early June to the end of July (maximum around the turn of the month) and once in mid-September. A plankton section between Pellinge and the bay of Lill-Pernåviken in August 1937 showed no lamellibranchs (Segerstråle 1939). In the easternmost part of the Gulf of Finland Sokolowa (1927) studied plankton between Peterhof and Tolbuchin from June to November 1923. No lamellibranch larvae were found.

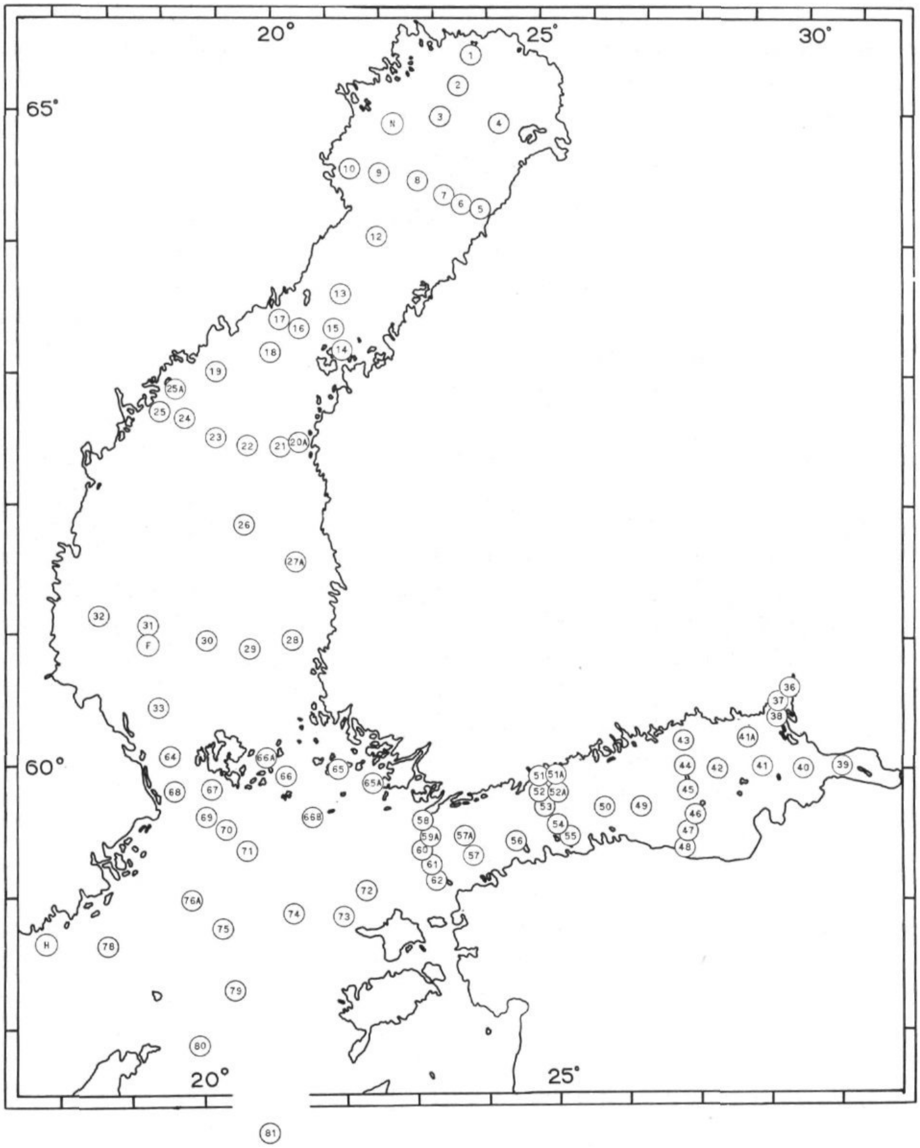

Fig. 4 Chart showing the F stations of the Baltic (1—81) and the permanent plankton stations during the years 1950—1953 (Norströmsgrund = N, Finngrundet = F, Hävringe = H, Jungfruskär = F 66, Helsinki = F 52 A).

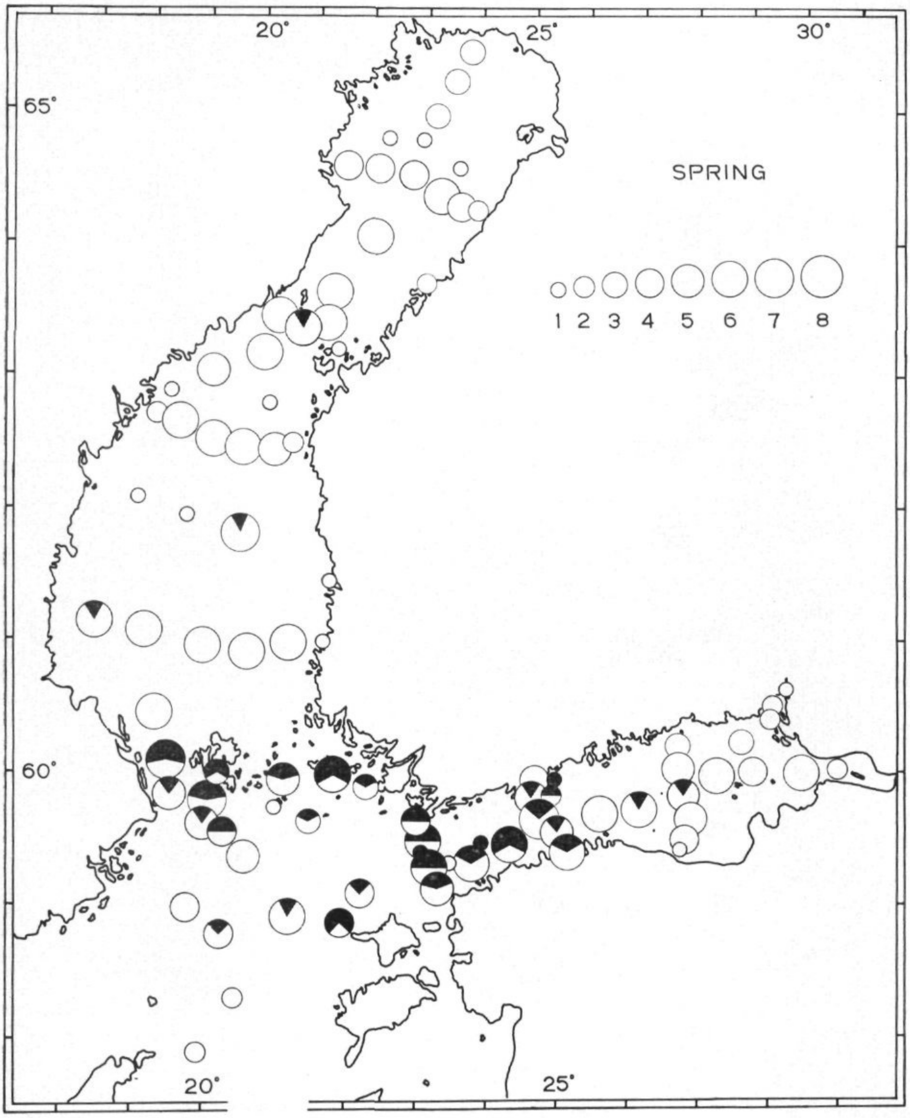

Fig. 5 The distribution and frequency of occurrence of lamellibranch larvae in spring in the northern Baltic area during the years 1903–1911 according to »Plankton-tables for Finland». The areas of the circles indicate the number of samples, viz. the number of springs when samples were taken (1–8). The black sectors indicate the percentage of samples containing lamellibranch larvae.

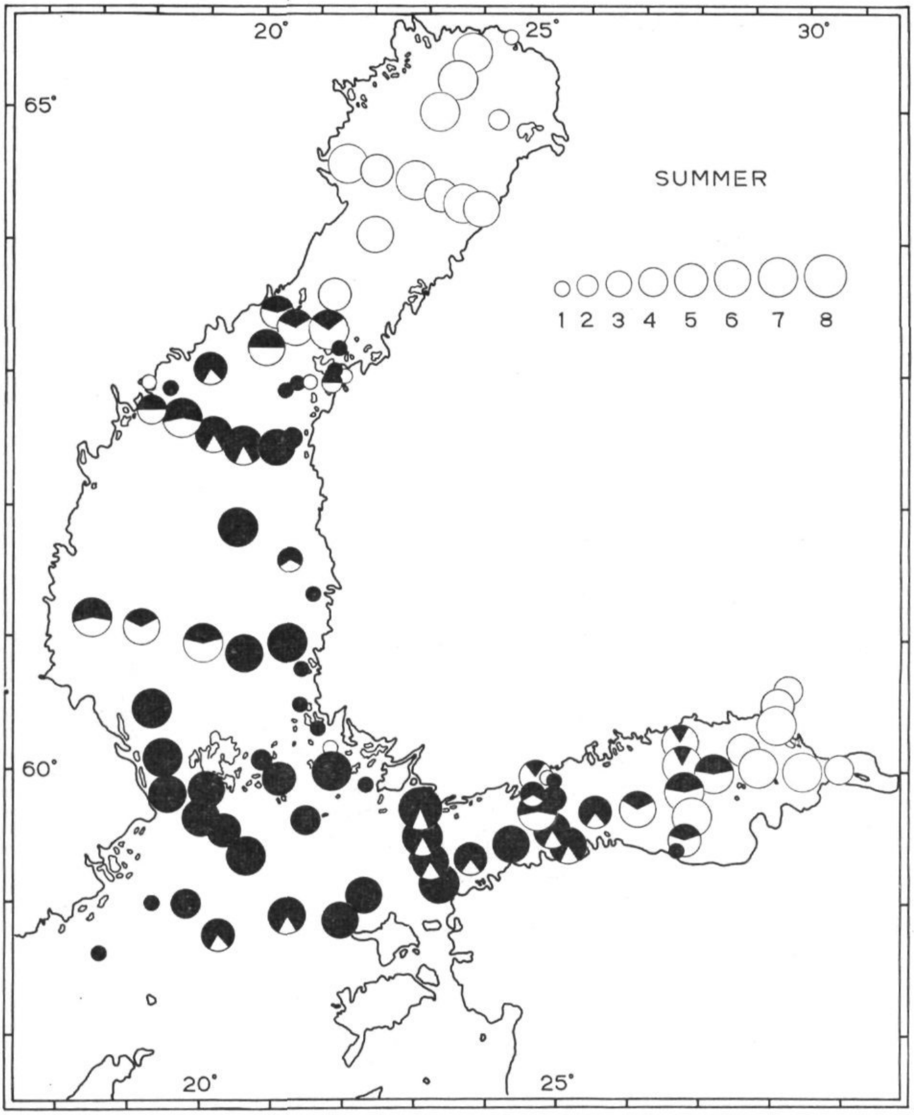

Fig. 6 The distribution and frequency of occurrence of lamellibranch larvae in summer in the northern Baltic area during the years 1903—1911 according to »Plankton-tables for Finland». Explanations as for Fig. 5.

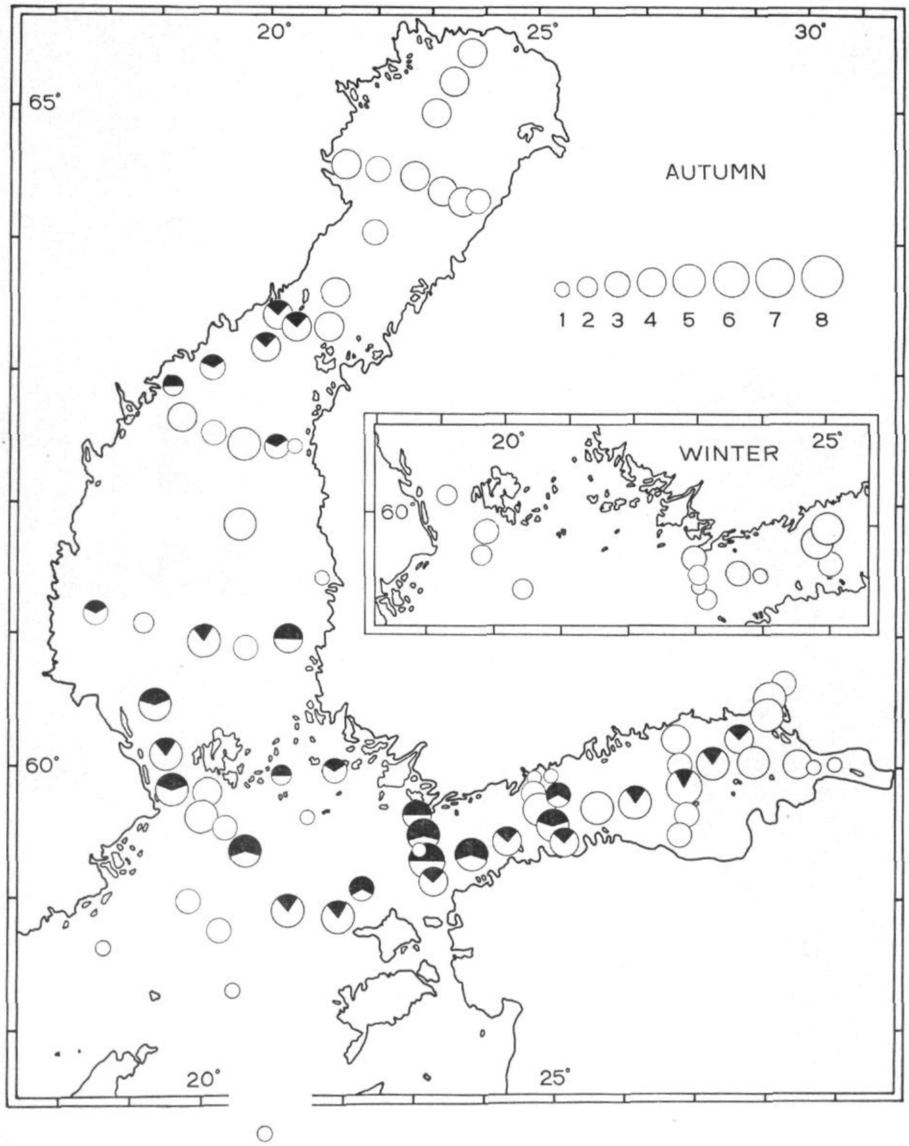

Fig. 7 The distribution and frequency of occurrence of lamellibranch larvae in autumn in the northern Baltic area during the years 1903–1911 according to »Plankton-tables for Finland». Explanations as for Fig. 5. The insert shows winter samples.

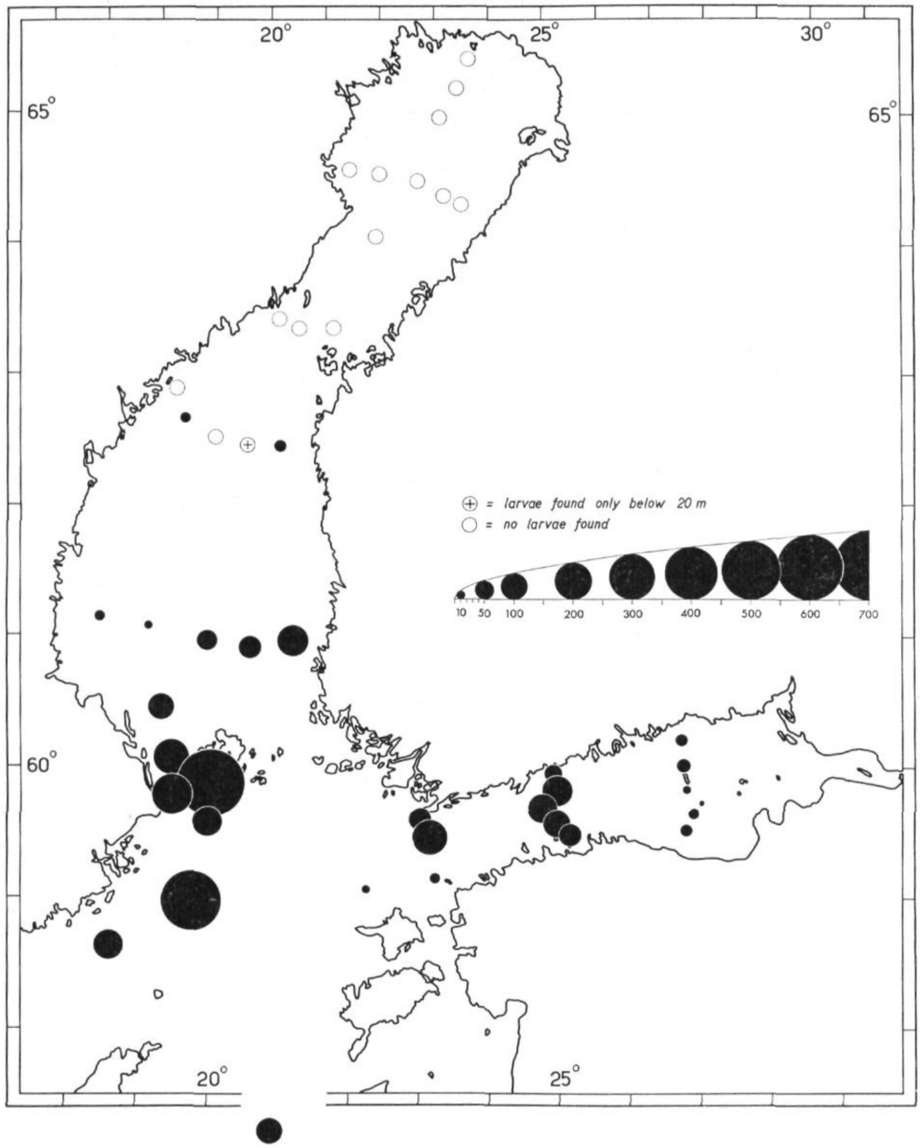

Fig. 8 Quantitative occurrence of lamellibranch larvae in the northern Baltic area during a cruise in July 1934. Number of larvae in the layer from the surface to 20 m depth, corresponding to a water volume totalling 100 litres per station (except at stations F 12 and F 23 where only 0–5 and 0–10 m respectively were sampled). The number of individuals is proportional to the areas of the circles. Drawn from the primary tables of Purasjoki (unpubl. tables, *a*). For chart of stations, see Fig. 4.

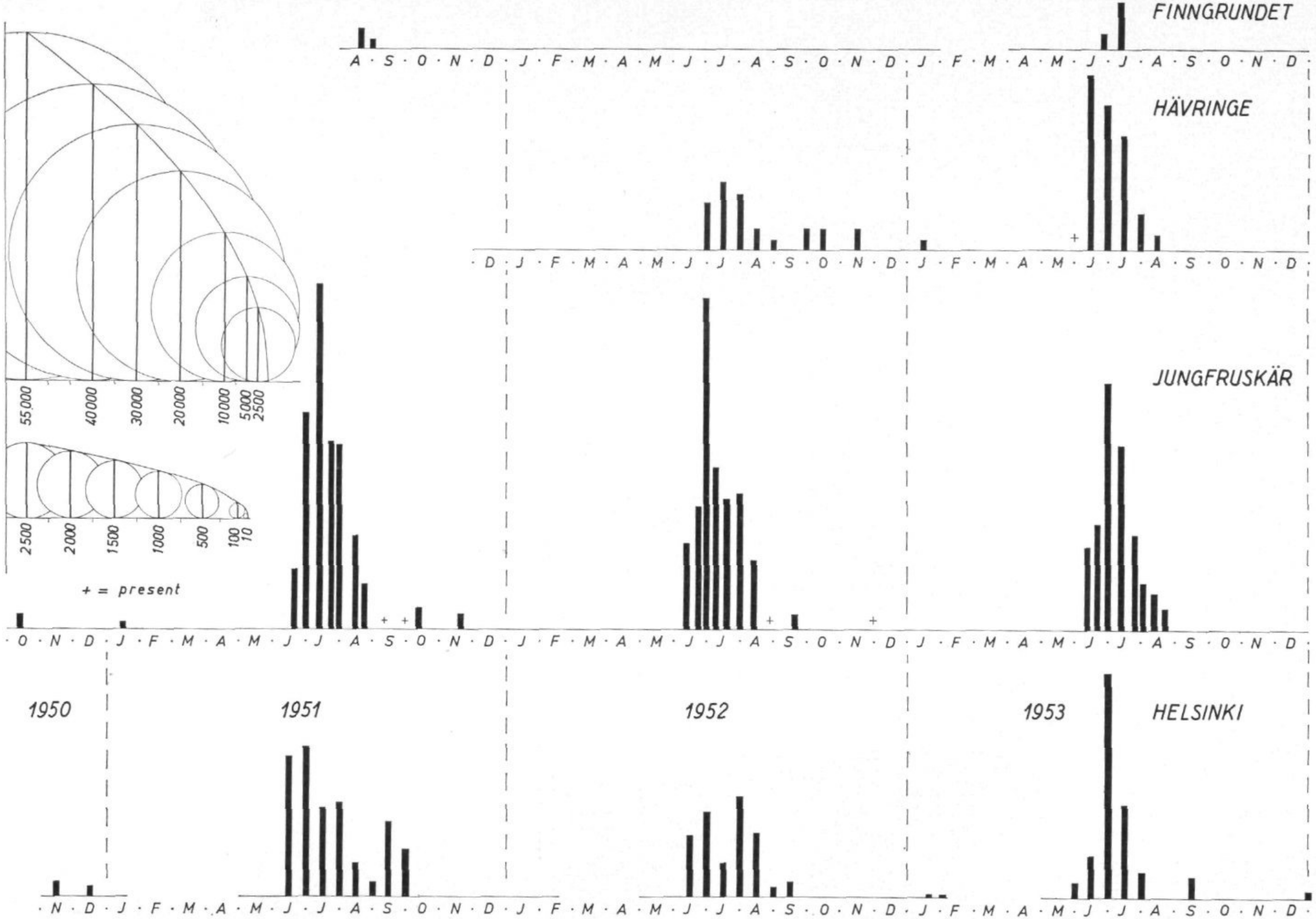

Fig. 9 Occurrence of lamellibranch larvae at five stations in different parts of the northern Baltic area during the years 1950—1953. The number of individuals per haul (25—0 m) is proportional to the areas of the circles, whose diameters are indicated in the diagram. For location of stations, see Fig. 4. Drawn from the primary tables of Purasjoki (unpubl. tables, *b*).

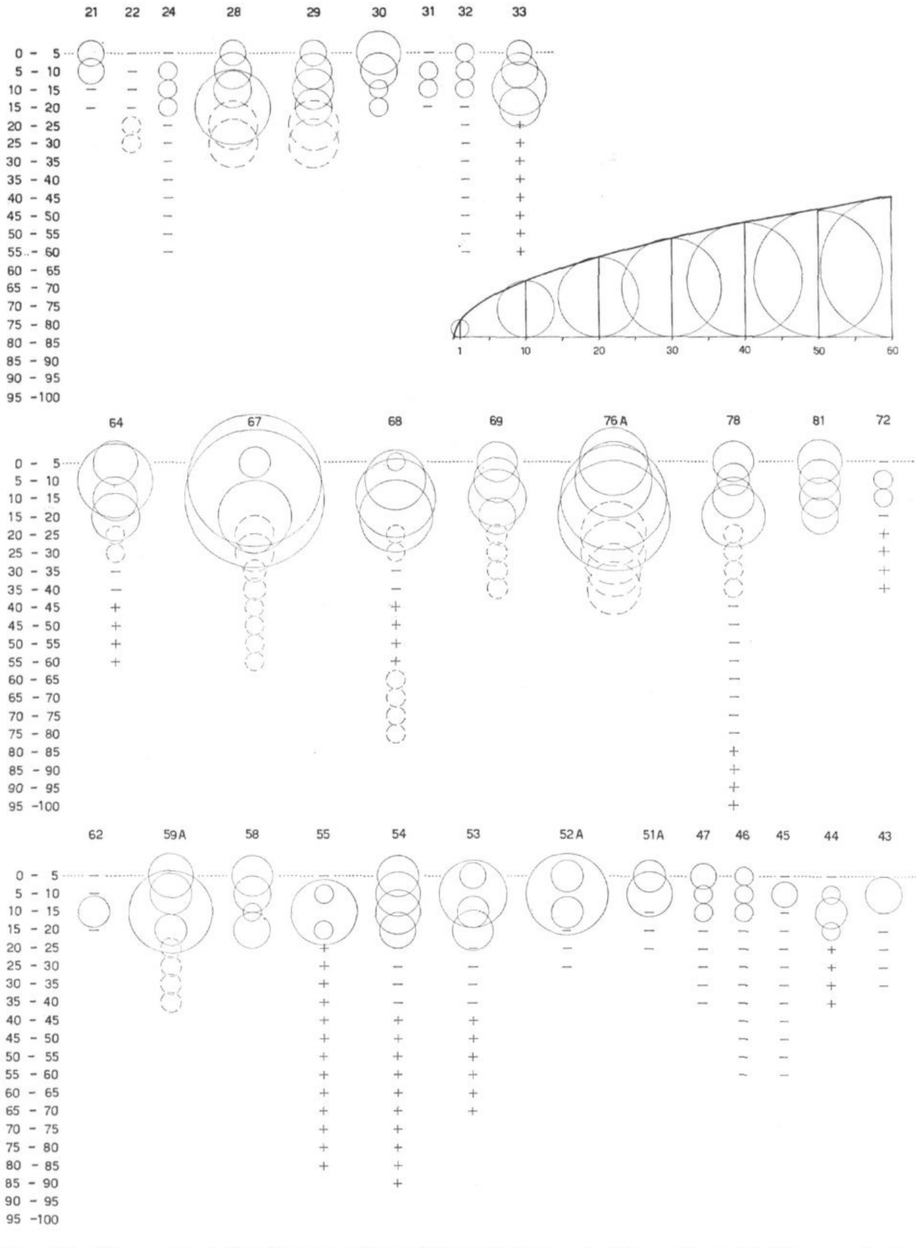

Fig. 10 The vertical distribution of lamellibranch larvae in the northern Baltic area during a cruise in July 1934. The number of larvae per vertical metre of the hauls. Each vertical m corresponds to a water volume of 5 litres sieved. The number of individuals is proportional to the areas of the circles. Dotted circles represent hauls more than 5 m in length. + = less than 1 ind./vertical m. First row: Bothnian Sea; middle row: Åland Sea and the northern part of the Baltic proper; bottom row: Gulf of Finland. For location of stations, see Fig. 4. Drawn from the primary tables of Purasjoki (unpubl. tables, *a*).

As regards the vertical distribution of the lamellibranch larvae in the northern Baltic area, they occur most abundantly, according to the tables of LEVANDER, in the uppermost 20 metres, though they were also found at depths exceeding 200 m. It is very difficult to obtain a more detailed picture of the vertical distribution from these tables, because the samples were taken with a variety of nets and from very different depths (cf. PURASJOKI 1958, p. 55). HESSLE & VALLIN (1934, Fig. 27) found bivalve larvae in the daytime from the surface to 100 m depth, mainly in the layer above 30 m. LINDQUIST (1958 *b*, p. 112) recorded them in the Bothnian Sea from the whole water mass, most abundantly in the layer above 20—30 m. In the area between Pojoviken and Tvärminne, HALME (1960, p. 87) found that the lamellibranch larvae occur both above and below the thermocline, but mainly in the epilimnion. According to this author, the larvae may show rather intense but irregular vertical migrations. In July 1934, according to the tables of PURASJOKI (unpubl. tables, *a*), the highest density of these larvae was found above 20—30 m. Often the greatest abundance was in the 5—15 m layer (Fig. 10).

DISCUSSION

As mentioned above, a discrepancy was found in the spring, according to LEVANDER's tables, in the distribution of lamellibranch larvae between the Bothnian Sea and the areas south of it. In this season the larvae very rarely occurred in the Bothnian Sea. There seems to have been a similar discrepancy between the eastern and western parts of the Gulf of Finland, where larvae occurred much more frequently in the western parts of the area (Fig. 5). Possibly the current conditions may be the reason for this phenomenon also (cf. p. 21). According to the »Atlas de Finlande» (1910) and WITTING (1912 *a*), which portray conditions on the basis of measurements simultaneous with the sampling for LEVANDER's tables, in June the currents flow southwards along both the west and east coasts of the Bothnian Sea, and westwards over almost the entire Gulf of Finland, viz. in the direction *from* the areas where the larvae were rare in this season. However, already in the 1925 edition of the »Atlas of Finland», a current chart is given for June showing an inward flowing current along the east coast of the Bothnian Sea and the south coast of the Gulf of Finland. But PALMÉN (1930, p. 12) stated that in early summer an outward current, due to strong inflow of fresh water and weak winds, is to be expected over the entire surface of the sea. Further he wrote that along the east coast of the Gulf of Bothnia and the south coast of the Gulf of Finland the current resultants are rather vague (»unbestimmt») in June, although the inward current probably dominates. There are however, according to the same author, years with an outward current in these areas. In the Gulf of Bothnia the tendency to an outward current is strengthened by N.W. winds in June. See also LISITZIN 1948, p. 13.

It is thus obvious that in the spring and early summer the tendency to inward flowing currents is less marked than in the summer and autumn, and there seem to be years or periods of years with an outward current dominating in the spring and early summer in the Bothnian Sea, and perhaps also in almost the entire Gulf of Finland. The discrepancies in the distribution of lamellibranch larvae in the spring, as observed from LEVANDER's tables, may at least partly be explained by this.

At present the general trend of the current systems seems to be known, but there are no investigations thorough enough to show the current pattern in detail during different seasons, and we do not know much about the variations from year to year. Unfortunately, there are no comprehensive investigations from recent years, either on currents or on plankton. The withdrawal of most of the lightships has considerably reduced the opportunities for such comparisons.

Another factor to reckon with in this respect is the earlier warming up of the Archipelago Sea and the western part of the Gulf of Finland compared with that of the Bothnian Sea and the eastern part of Gulf of Finland (cf. WITTING 1912 *a*, Table I: 1—2), giving rise to earlier spawning.

On the basis of the information now available it can generally be established that lamellibranch larvae begin to occur in plankton (Table II) in May—July in the Bothnian Sea, in May—June in the Åland Sea, the northern part of the Baltic proper and the Gulf of Finland, depending on the rise of temperature, the time of which may fluctuate considerably from year to year. Also the fluctuations in abundance may be considerable. In the spring the larvae appear earlier in the archipelago and coastal waters than in the open sea, partly owing to the earlier warming up of these waters and partly to the fact that the main production areas are in shallow water, viz. mainly in the archipelago or close to the coast. Also the time of maximum abundance of the larvae fluctuates: it seems to occur in July—August in the Bothnian Sea, and in the other parts of the northern Baltic area in June—August, mostly in June—July. HESSLE & VALLIN (1934, p. 57) found that in the Central Baltic the maximum abundance of larvae occurred later in the open sea than in the archipelago and near the coast. A corresponding tendency also appears, for example, in a comparison between Utö and Hangö (see LEVANDER & PURASJOKI 1947, Diag. 33, p. 50). After the height of the season larvae may occur in small quantities to the end of the year or somewhat later. At least in the Gulf of Finland they may sometimes still occur even in early February.

According to LEVANDER & PURASJOKI (1947, p. 29), the abundance

Table II. Occurrence of lamellibranch larvae during different months of the year in the northern Baltic area. Drawn: main occurrence. (From various sources, cf. the text.)

	J	F	M	A	M	J	J	A	S	O	N	D
Bothnian Sea					..	...	▬▬▬	▬▬▬	...	...	...	
Archipelago Sea & the northern Baltic proper	..				..	▬▬▬	▬▬▬	▬▬▬	...	...	...	...
Gulf of Finland	...	.			...	▬▬▬	▬▬▬	▬▬▬	...	...	...	...

of larvae in the summer is followed by a low period in September, after which larvae may occur again untill December. The plankton tables (Hävringe, Jungfruskär, Helsinki, cf. p. 17) which Dr. PURASJOKI (unpubl. tables, *b*) has placed at my disposal give further proof of the existence of such a rather regular depression in the autumn. A hint of the same thing is given by Fig. 2 in HALME's (1958) paper on the zooplankton of Pojoviken and adjacent areas. In the outer parts of the area (»Meergebiet») there is a gap in the occurrence of lamellibranch larvae in the epilimnion from the end of August to the end of September.

Hence, a more or less marked transient low period seems to be the rule, at least in the northern Baltic proper and the Gulf of Finland. LINDQUIST (1959) does not give any information to indicate such a depression in the Bothnian Sea. However, his samples are not quite suitably distributed in time to give information of this kind. Finally, as far as the fixed plankton station Finngrundet in the southern part of the Bothnian Sea (Fig. 9) is concerned, lamellibranch larvae occurred in too small numbers to illustrate this question; in fact, in autumn none were found at all.

The problem is to find the reason for the depression. There are two conceivable reasons for this. One could be a second spawning period in shallow water for some species. Another reason could be the uneven warming of the water at different depths, an assumption which is supported by THORSON's (1946) investigations in the Sound. Amongst marine invertebrates the temperature is very often the primary factor controlling the maturation of the genital products and the spawning (see e.g. MOORE 1958). A characteristic of the yearly temperature cycle of the sea is that the surface layer warms up at first, and a thermocline ensues. During the summer this thermocline proceeds downwards owing to turbulent mixing. As the shallow waters warm up first, the shallow-water populations of lamellibranchs may spawn earlier than deep-water populations of the same species. In late summer, normally from August to September, the whole population above the thermocline has spawned and the number of larvae greatly decreases or they totally disappear from the plankton. Perhaps the spawning in the upper layers will be interrupted by the temperature fall. The result is, in any case, a decline of the number of larvae, this being the autumn depression. On the other hand, the population beneath the thermocline will not yet have spawned. The air temperature has fallen and the water above the thermocline has cooled. Owing to the reduced temperature difference between the water masses separated by the thermocline the stability of the stratification is reduced, and a period of strong winds can soon depress the thermocline, or eliminate it. The temperature of the surface water is lower than before, it is true, but the temperature of the deep water is higher. Now the deep water populations may spawn. Consequently such a spawning would offer an explanation for the larvae in the autumnal plankton.

Practically the whole population of *Cardium* and *Mya*, and most of the *Macoma* and *Mytilus* populations, live in shallow water. Accordingly, these populations give rise to the summer maximum of larvae. In the northern Baltic area *Macoma* is the only lamellibranch which forms noteworthy, though sparse, populations in deeper water, for which reason it is to be expected that the lamellibranch plankton late in the autumn would consist almost exclusively of *Macoma* larvae (possibly with elements of *Mytilus* larvae). My observations on lamellibranch larvae in the late autumn and winter plankton bear out this hypothesis. That the length of the larval life in marine invertebrates is often markedly dependent on the temperature is well-known (see e.g. Loosanoff & Davis 1963; for further references see Thorson 1946, p. 452, Moore 1958, pp. 24—25). Whether there is a prolonged larval stage with subsequent normal metamorphosis in the case of the autumn and winter larvae of the Baltic at the prevailing low temperature, or whether they perish during the larval stage before metamorphosis, is not known. Whether or not the food supply for the larvae in winter will be critical is likewise unknown. Most of the larvae that I have observed in late autumn and in winter have been small and transparent, and no spatfall has been recorded after September. This indicates that these late larvae will perish, at least to a very large extent, before they can undergo metamorphosis.

If we finally compare the distribution of postlarval lamellibranchs with the distribution of larvae we find, especially in the Gulf of Bothnia, a marked incongruity. *Macoma* seems to occur at least periodically as far as the area of Hailuoto in the northern part of the Bothnian Bay, but lamellibranch larvae have never been found north of the Quark (cf. pp. 8 and 18). A corresponding discrepancy is found in the eastern part of the Gulf of Finland, though it is considerably smaller than that in the Gulf of Bothnia. The reasons might be in part that the innermost areas of the Gulf are imperfectly studied, in part that the most extensive investigations happened to take place during periods of low salinity. As far as Norströmsgrund (cf. p. 17) is concerned, regular samples have certainly been taken during the period of increased salinity, but the geographical position is too far north in the area of low salinity to expect any regular occurrence of lamellibranch larvae. Of our marine bivalves *Macoma* is the only one which occurs in the Bothnian Bay, and even so very sparsely (see HESSLE 1924, SEGERSTRÅLE 1962). SEGERSTRÅLE (op. cit., p. 18) has suggested that the strong inflow of humic substances from the rivers into the Bothnian Bay may have an adverse effect upon the species. Determinations of the pH of the surface layers of the Baltic (Table I) show low values for the Bothnian Bay (BUCH 1945). Because the conditions are unfavourable and the population small, it can be assumed that the production of larvae in the zone of the inner limit of the species is small, especially in the Bothnian Bay. Against the background of the plankton investigations which have been performed, and with a knowledge of the great fluctuations of spatfall and population density even in the main distribution area of many species, it seems probable that larvae do not occur every year near the innermost parts of the ranges of the marine lamellibranchs in the Baltic. Possibly the conditions near these limits are favourable only in certain years and then the local population can spawn.

If the population at the extreme limit seldom or never spawns, the population is partly or totally dependent on larvae transported from areas with more favourable conditions (cf. KINNE 1964). The answers to these questions can only be obtained from detailed studies at the inner limits of distribution.

Acknowledgements. I am deeply indebted to Prof. SVEN G. SEGERSTRÅLE, Head of the Biological Laboratory of the Institute of Marine Research, for encouragement and valuable discussions, and to Dr. K. J. PURASJOKI, for kind permission to use his unpublished plankton tables and for his readiness to be of assistance. Further I wish to express my gratitude to the staff of the Institute of Marine Research, especially to Mr. SVANTE NORDSTRÖM, M.Sc., for discussions on the hydrography of the northern Baltic area; to Mr. ROBIN SOUTH, B.Sc., Liverpool and to Mr. S. NORDSTRÖM for linguistic help, and to Mrs. J. M. PERTTUNEN, B.Sc., for the final revision of the English manuscript.

Summary

A survey is given of the distribution of the lamellibranchs *Mytilus edulis* L. *Cardium lamarcki* Reeve, *Macoma baltica* (L.) and *Mya arenaria* L. in the northern Baltic area. Factors controlling the distribution are discussed. The larval and postlarval stages are treated separately.

In the Gulf of Bothnia lamellibranch larvae are recorded from the

Bothnian Sea and the Quark, but have never been found in the Bothnian Bay, although postlarval *Macoma* occurs high up in the area, at least periodically. In the Gulf of Finland lamellibranch larvae are found as far east as 28°E.

In the Bothnian Sea one finds a tendency in the summer and autumn to greater abundance and more regular occurrence of lamellibranch larvae in the eastern than in the western parts. The difference is suggested to be due to a transport of larvae by currents, and to a difference in the production of larvae owing to different topographic and hydrographic conditions.

Reviewing the entire northern Baltic area, larvae are found most regularly and in greatest numbers in the southwest, viz. the Åland Sea, the Archipelago Sea, the northern part of the Baltic proper and at the entrance to the Gulf of Finland, which is to be expected from the hydrographic conditions and the distribution of the postlarval stages.

Bivalve larvae are found to occur in plankton from May to January—February, with their maximum abundance in June—August. A more or less marked transient low period in the occurrence of larvae in the autumn, mentioned in the literature, seems to be the rule, at least in the northern Baltic proper and in the Gulf of Finland.

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Communicated January 18, 1965 by S. G. Segerstråle
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